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Vestibular contribution to the planning of reach trajectories

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Abstract Reaching for an object while simultaneously rotating induces Coriolis and centrifugal inertial forces on the arm that require compensatory actions to maintain accuracy. We investigated whether the nervous system uses vestibular signals of head rotation to predict inertial forces. Human subjects reached in darkness to a remembered target 33 cm distant. Subjects were stationary, but experienced a strong vestibular rotation signal. We achieved this by rotating subjects at 360°/s in yaw for 2 min and then stopping, and subjects reached during the ‘post-rotary’ period when the deceleration is interpreted by the vestibular system as a rotation in the opposite direction. Arm trajectories were straight in control trials without a rotary stimulus. With vestibular stimulation, trajectory curvature increased an average of 3 cm in the direction of the vestibular stimulation (e.g., to the right for a rightward yaw stimulus). Vestibular-induced curvature returned rapidly to normal, with an average time constant of 6 s. Movements also became longer as the vestibular stimulus diminished, and returned towards normal length

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Keywords Vestibular system · Reaching · Motor control · Inertial forces · Coriolis · Centrifugal

Introduction

Accurate reaching requires the nervous system to compensate for forces that act on the arm during movements. Researchers have studied central nervous system compensation for interaction torques, i.e., the forces on a joint that occur due to the motion of other joints (Gribble and Ostry 1999; Hollerbach and Flash 1982; Sainburg et al. 1995), and the effects of natural forces like gravity (Augurelle et al. 2003; Papaxanthis et al. 2003; Fisk et al. 1993). Other researchers have applied artificial force fields while performing reaching movements when subjects held the handle of a robotic arm (Shadmehr and Mussa-Ivaldi 1994). These studies indicate that humans rapidly adapt to novel forces and plan movements to compensate for expected forces.

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If we reach while simultaneously turning, such as during an active turn-and-reach movement or if our environment (car or plane) rotates, any movement that has a component perpendicular to the axis of rotation is subject to Coriolis and centrifugal forces. The Coriolis force is $2m(\vec{v} \times \vec{\omega})$, where m is mass, $\vec{\omega}$ is the angular velocity, and \vec{v} the linear velocity. For example, if a subject rotates to the left while reaching forward, the Coriolis force is directed to the right. Additionally, rotation produces a centrifugal force $\omega^2 \vec{r}$, where \vec{r} is the distance from the rotation axis.

People rapidly adapt to novel inertial forces. Lackner and DiZio extensively studied motor adaptation in a rotating environment (DiZio and Lackner 1995, 2001; Lackner and DiZio 1994, 1998a, b), under conditions where subjects did not perceive the rotation. These studies found that when first placed in the rotating environment, reaching movements are curved as a result of the Coriolis forces, but subjects very rapidly adapt and movements soon have normal kinematics. Similarly, Nowak et al. (2004) measured grip forces when subjects moved an object in a rotating chamber, and found that subjects quickly adapted their gripping force to the Coriolis and centrifugal forces.

Reach paths during active turn-and-reach movements suggest that the nervous system anticipates the effects of Coriolis forces (Pigeon et al. 2003). The nature of this prediction is not fully known. The motor system could alter reaching movements during body turns without explicitly predicting inertial forces. For example, the reach command could be altered if a concomitant body turn is also programmed or sensed via efference copy of the motor command, which would be an effective strategy for active turns but would fail for passive rotations, such as in vehicles. Short latency corrective movements could play a role, although they are unlikely to be the sole source of compensation, because reaching trajectories are still altered by Coriolis forces during passive rotation (Lackner and DiZio 1998a, b; DiZio and Lackner 2001). Alternatively, sensory signals of body rotation could be used along with an internal estimate of arm mass to predict inertial forces, which would be useful for both active and passive rotations. Cohn et al. (2000) found that when visual information about whole-body rotation is present, arm movements are altered in a manner consistent with the hypothesis that the nervous system uses visual signals to predict Coriolis forces.

Strong sensations of body movement also come from vestibular stimulation, a major source of information about our movement and orientation in space. Vestibular signals are known to affect reaching movements (Karnath et al. 1994; Mars et al. 2003; Bresciani et al. 2002a), which could be accomplished either through changes in the perceived egocentric target location, or by a mechanism that seeks to stabilize the arm in space (Bresciani et al. 2005),

analogous to the vestibular ocular reflex which stabilizes the eye in space. Here, we investigated if vestibular signals are used by the nervous system to predict the consequences of Coriolis and centrifugal forces on reaching movements.

Materials and methods

The experimental protocols were approved by the ethics committee at Zürich University Hospital and adhered to the Declaration of Helsinki for research involving human subjects. Six subjects participated in these experiments, and all gave their informed consent prior to participating. The three subjects in the first experiment included both authors, and three different subjects participated in the second experiment.

Apparatus

Subjects sat in a motorized rotating chair (Acutronic, Switzerland), operated with AcutrolTM software and hardware, and interfaced with LabVIEWTM software (see Fig. 1a). The earth-vertical rotation axis used in these experiments bisected the subject's inter-aural axis. Subjects were comfortably seated in the chair and secured with safety belts. Individually adjusted masks (Sinmed BV, Reeuwijk, The Netherlands), made of a thermoplastic material (PosicastTM), were moulded to the head after warming. The mask was attached to the back of the chair and restricted the head movements. The head was tilted slightly forward to ease viewing of a horizontal surface attached to the chair where we projected target spots with a red laser under computer control. A tactile stimulus located

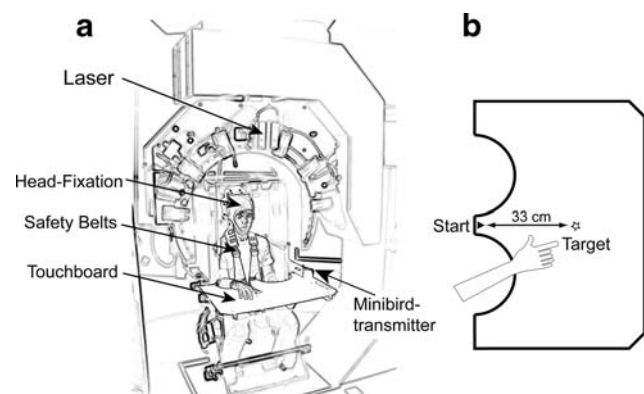


Fig. 1 **a** The motorized turntable showing the subject with safety and head restraints, and the touch board. **b** Top view of the touch board. A tactile stimulus was placed on top of the board near the subject, so the hand could be properly positioned before each trial in darkness. A laser was mounted above the subject, and projected a target spot 33 cm in front of the start position

10 cm in front of the subject was the starting point of each movement (Fig. 1b).

The three-dimensional position of the pointing finger was measured at 103 Hz with a MiniBird system (Ascension-Technology). The sensor was attached to the top of the fingernail with tape, and the finger of a latex glove was worn over the sensor to increase the friction of the finger when it touched the board.

Procedure

We conducted two experiments, both in the dark. In the first, we measured reaching with the preferred hand with rightward and leftward vestibular stimulation. In the second experiment we compared reaching with preferred and non-preferred arms. Both experiments used two types of trials. In *control trials*, subjects made normal reaching movements while stationary. In *vestibular stimulation trials* the subject experienced a strong vestibular signal that they were rotating, when in fact they were stationary. This allowed us to measure the effects of the vestibular stimulation without any rotation-induced forces acting on the arm.

Each movement began with the pointing finger ~10 cm in front of the subject (see Figs. 1b, 2a). The target was a red laser spot projected 33 cm in front of the starting point for 5 s. Five seconds after the spot was extinguished, a tone cued the subject to touch the board at the remembered target location. A second tone of different pitch presented

1.5 s later instructed the subject to return the finger to the starting position. Subjects were cued to reach every 4 s, for 60 s. We instructed them to move quickly but accurately, and to hold their finger in the final position until the next auditory cue.

For vestibular stimulation trials, we used a method common in vestibular studies to produce a rotation signal from the vestibular system, when in fact the person is stationary. This situation provides us with the opportunity to study compensation for expected inertial forces, when in fact none are present. When people are suddenly stopped after a sustained, constant velocity rotation, the subject perceives a strong feeling of rotation in the opposite direction despite the fact that they are stationary. This ‘post-rotary’ response arises as a consequence of the mechanics of the vestibular canals. During head acceleration the inertia of the endolymph fluid leads to a displacement of the cupula membrane. This in turn bends the vestibular hair cells, resulting in neural activity in the vestibular nerve (Hain et al. 2000). The high viscosity of the endolymph mechanically converts the acceleration signal into a signal that is initially proportional to head velocity. For longer-duration rotations, however, the mechanical elasticity of the cupula pulls it back to the resting position (Wilson and Melvill 1979). As a result, during a constant-velocity rotation, the vestibular canals signal a head rotation only for 30–60 s. (More specifically, the cupula returns to the resting position with a time constant of ~6 s, i.e., after 6 s the deflection of the cupula has

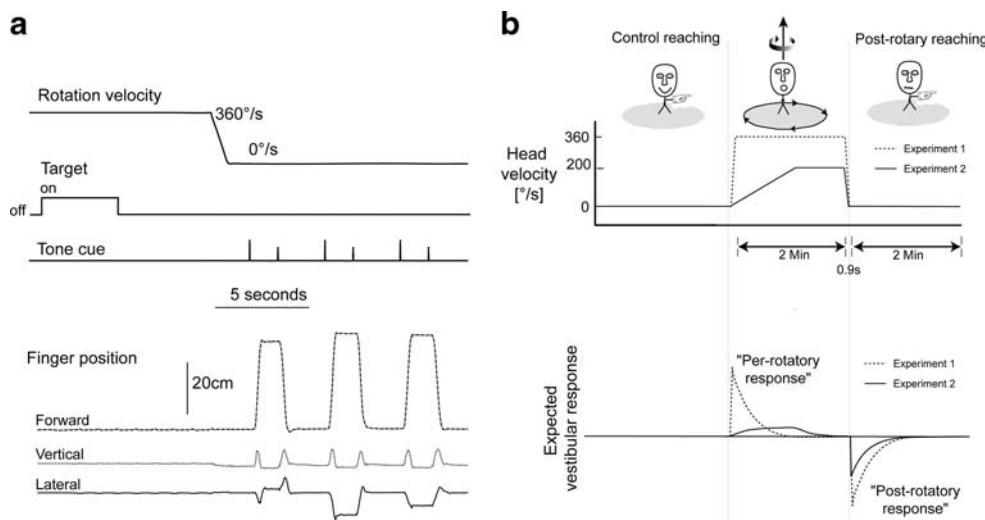


Fig. 2 **a** The structure of post-rotary reaching trials and example data are shown. While the subject was rotating, but feeling stationary, the visual target was shown for 5 s. One second after the rotation ended, the subject was cued with a tone to reach to the remembered target location. A second, lower-pitched tone cued the subject 1.5 s later to return the hand to the start position. **b** *Top* The general trial procedure showing the sequence of control reaching trials, rotation, and post-

rotary reaching. *Bottom* The expected vestibular response is shown for both experiments. The semi-circular canals respond to the head acceleration, and with constant velocity rotation the signal from the canals decays with an exponential time course. Including ‘velocity storage’, we assumed a time-constant of 15 s for this sketch. With deceleration, the canals will signal a rotation in the opposite direction, which again decays

decreased by $1/e$ ($\approx 37\%$). A neural processing mechanism called ‘velocity storage’ extends this time constant for yaw rotations to about 15 s; Raphan et al. 1979.) A subsequent deceleration stimulates the vestibular system in a similar manner as the initial acceleration, although in the opposite direction (the ‘post-rotary’ response), and so subjects perceive they are rotating even though they are in fact stationary. Note that this stimulus produces a head rotation signal that is similar to that produced by real head rotations. Other methods of producing vestibular sensation in the absence of real movement, e.g., calorics or galvanics, induce stimulation patterns that cannot occur naturally and produce strong sensory cue-conflicts between the semi-circular canals and otolith organs.

All our data were collected when subjects were stationary. We use the terms ‘rightward yaw’ and ‘leftward yaw’ stimulation to indicate the direction of rotation as indicated by the semi-circular canals during the post-rotary period. As discussed above, the post-rotary canal stimulus is always in the opposite direction as the earlier rotation direction.

In the first experiment, subjects were rotated about the earth-vertical axis (yaw) at $360^\circ/\text{s}$ for 2 min, and then suddenly stopped with a deceleration of $400^\circ/\text{s}^2$ (Fig. 2b). Ten seconds before the end of rotation, when subjects feel stationary, the target was shown for 5 s. One second after stopping they received the first tone cue to reach to the remembered target. They were told to reach as if the target moved with them, like reaching for an object inside a moving automobile. These instructions eliminated ambiguities of commands like ‘point straight ahead’, which could either be interpreted with respect to the subject, or with respect to the surrounding space.

With repeated exposure this very strong motion stimulus can be nauseating, so we usually limited our sessions to one rotation in each direction, with a recovery period in-between to allow the subject to recover and re-establish normal reaching behaviour. Each subject completed 4–6 sessions, and we typically waited 5–6 days between sessions.

In a second set of experiments, in which we compared reaching with preferred and non-preferred arms, we made several changes to the protocol in order to increase subject comfort. The rotation velocity was lowered to $200^\circ/\text{s}$, and was reached by accelerating slowly ($3^\circ/\text{s}$). Subjects were rotated at a constant velocity for 55 s before stopping abruptly, as in experiment 1, with a deceleration of $400^\circ/\text{s}^2$. Subjects rotated to the right when reaching with the right arm, and to the left when reaching with the left arm, so that the expected Coriolis force direction was always towards the body midline, thereby controlling for mechanical differences in the right- and left-arms’ lateral movement. In each experimental session, subjects completed one trial with the dominant and one trial with the non-dominant arm, and the order was alternated each session. Two of the

three subjects were right-handed, and because the mirrored data from the left-handed subject were similar to the data from the right-handed subjects, we converted the data so that all subjects appear as right-handed.

We can estimate the expected Coriolis and inertial forces based on the vestibular stimulation with a few assumptions. For a typical subject, we estimated the mass and centre-of-mass of the forearm and hand based on the methods of Winter (2005). In our example, the mass estimate is 1.54 kg, and the centre-of-mass is 29 cm from the elbow. Figure 3 shows the movement of the centre-of-mass of the forearm during a straight reaching movement, with the position shown in Fig. 3a, and the velocity in Fig. 3b. We then estimated the Coriolis and centrifugal forces that would act on the forearm if this exact reaching movement was performed while rotating in yaw at $360^\circ/\text{s}$ (Fig. 3c). Notice that the Coriolis force would very closely follow the forward-component of the velocity in Fig. 3b, and reaches a peak of 15.6 Newtons (N, kg m/s^2). The centrifugal force closely follows the forward position curve in Fig. 3a (the distance from the rotation axis), and changes from about 6

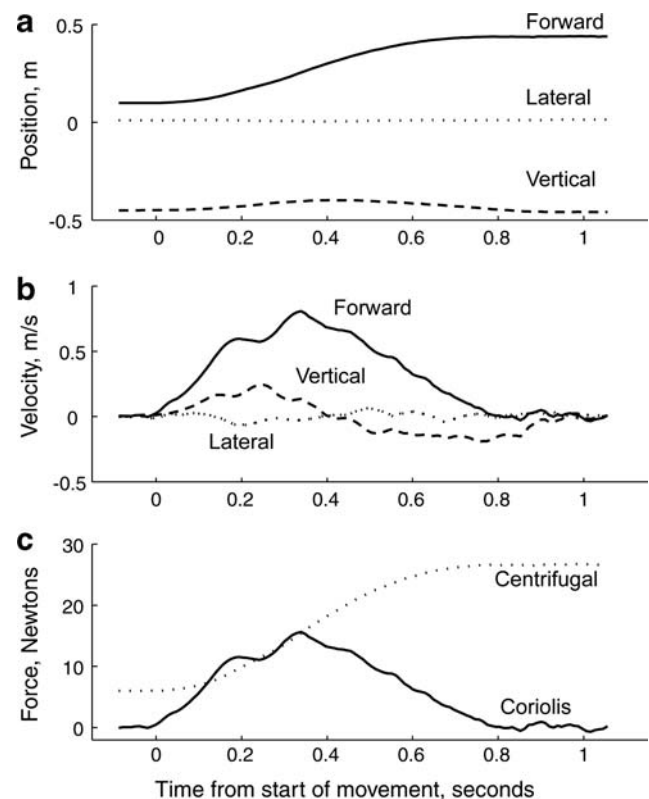


Fig. 3 An example reaching movement and expected Coriolis and centrifugal forces. An actual movement of the forearm is shown in **a** (position) and **b** (velocity), performed when the subject was stationary. If this exact movement was performed when the subject was rotating at $360^\circ/\text{s}$ about the yaw axis, the Coriolis and centrifugal forces that would be generated on the forearm (mass = 1.54 kg) are shown in **c**

to 27 N at the end of the reach. The magnitude of the Coriolis force is proportional to the rotation velocity, so if the rotation velocity was $200^\circ/\text{s}$ a peak force of 8.7 N would occur. The centrifugal force is proportional to the square of the rotation velocity, so decreasing the rotation velocity to $200^\circ/\text{s}$ would decrease the minimum and maximum centrifugal forces to 1.9 and 8.2 N, respectively.

Analysis

All data were analysed offline with MatLab software (The MathWorks, Boston MA, USA). We identified the onset and the end of reaching movements with a velocity criterion (5% of the maximum total velocity). The final finger position was taken 250 ms after velocity dropped below that criterion. Curvature was defined as the maximum perpendicular (lateral) distance from a line connecting the start and end points of the movement. To determine how curvature changed as a result of vestibular sensation, we determined the ‘vestibular induced curvature’ (VIC): for each subject we calculated the average curvature on all control trials, and subtracted this from each vestibular stimulation trial. Similarly, we computed the vestibular induced lateral and distance errors. ANOVAs were computed using the General Linear Model procedure in MINITABTM, multiple linear regressions with dummy variable coding for categorical data (e.g., dominant, non-dominant arm) were computed according to Kleinbaum et al. (1988), and exponential curves were fit to data with the *nlfit* function (least-squares fitting with the Gauss–Newton method) in MatLab.

Results

Experiment 1: reaching trajectories depend on the direction of vestibular stimulation

Hand paths during trials without vestibular stimulation were generally very straight, consistent with previous reports (Goodbody and Wolpert 1999; Morasso 1981; Abend et al. 1982). The average curvature (and standard deviation) for each subject was -0.16 (0.5), -0.7 (0.5), and -0.05 (0.3) cm. Reaching movements on control trials lasted an average of 743 ms, with maximum forward velocities of 91 cm/s, and subjects reached on average 1.6 cm short and 1.7 cm left of the target. During rightward and leftward yaw vestibular stimulations, the mean durations were 670 and 710 ms, and the average maximum forward velocities were 97 and 89 cm/s.

Figure 4b shows the reaching movements for the first five trials in control, rightward and leftward yaw stimulation experiments in one subject. The control trials (left column) are typically straight, and in this experiment the

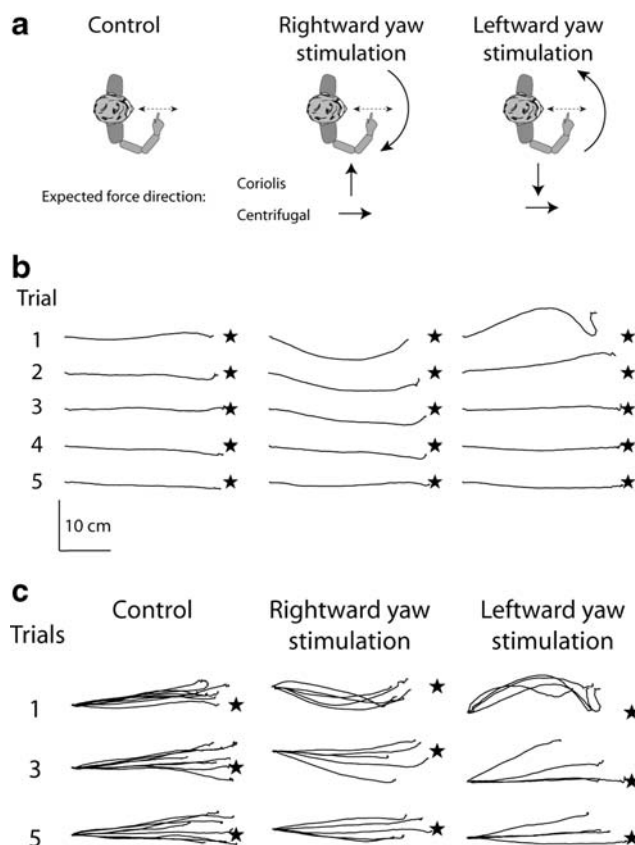


Fig. 4 **a** Schemas depicting the direction of stimulation and the expected force directions are shown for the three experimental conditions. The curved arrows in the sketches at the top indicate the direction of the sensory rotation cue. **b** Top view of reaching trajectories for the first five trials is shown for subject TH for control (left column), rightward stimulation (middle) and leftward stimulation (right) conditions. Reaching movements were made towards a remembered target (indicated by the star). **c** All 1st, 3rd, and 5th trials, for the same subject

subject tended to under-reach. With rightward yaw stimulation (middle column), the initial trajectory of the first trial is to the right, but the finger curves back towards the target. The second trial is also curved in the same direction, but to a lesser degree, and subsequent trials are straighter. With leftward yaw stimulation (right column), the initial movement is to the left, and the path then curves back towards the target. In this trial there are additional corrective movements towards the end of the reach. Later trials are considerably straighter. Figure 4c shows all the 1st, 3rd, and 5th trials for the same subject.

The VIC is shown in Fig. 5a for a different subject. This subject had an average VIC for the initial trials of 4 and -2 cm, for rightward and leftward stimulation conditions, respectively. The VIC is in the direction of the semi-circular canal yaw rotation signal, as if subjects were attempting to compensate for the expected Coriolis force. Average VIC declined for later reaches, and by the 4th

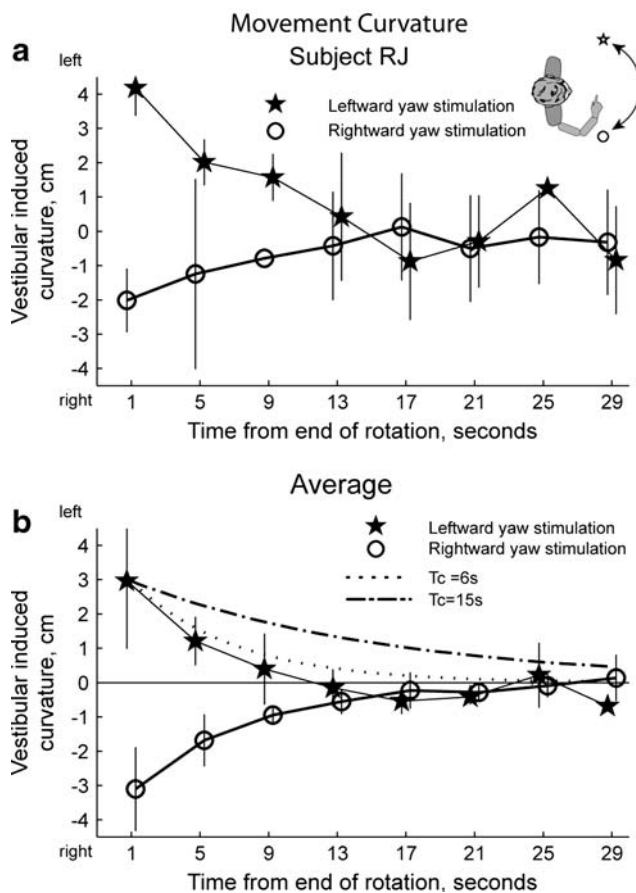


Fig. 5 **a** Average vestibular induced curvature (VIC) for subject RJ. Each point is the mean of 4–6 reaches, and error bars are ± 1 standard deviation. Points have been offset slightly from the actual time for clarity. **b** Average VIC across all subjects. Each point is the average of three subjects, and the error bars are ± 1 standard deviation. Also shown is the expected decline in curvature (for the leftward yaw stimulation condition) if the decay was due to the change in response of the vestibular canals alone [6 s time constant (T_c), dotted line] or the response including velocity storage (15 s, dash-dot)

reaching movement (13 s after the end of rotation), curvature is similar to control trials. The same was true for the average VIC across subjects (Fig. 5b). The average VIC on the first reaching movement was 3.0 cm for leftward yaw, and -3.1 cm for rightward yaw stimulation. An ANOVA on the first trial found a significant effect of the direction of vestibular stimulation on the VIC ($F(1,19) = 19.4$, $P < 0.005$). Exponential fits to the curvature data found time constants for the decline in curvature of 5.2 and 7.0 s for leftward and rightward vestibular stimulation conditions. Figure 5b also shows the expected decline in curvature (for the leftward yaw stimulation condition) if the decay was due to the change in response of the vestibular canals alone (6 s time constant) or the response including velocity storage (15 s). The decay in curvature is close to the decay time of the canals alone.

The change in curvature could be either due to the declining vestibular stimulation or to a change in expected Coriolis force if reaching velocity changed. Recall that the Coriolis force is proportional to both the rotational velocity and the reach velocity of the arm. Therefore, we looked for trends in peak forward arm velocity by computing linear fits to the average peak velocity versus time from the end of rotation. There was no significant change in peak velocity for leftward yaw stimulation (slope = $0.012^\circ/\text{s}$ per second; $P > 0.8$), but there was a small decrease in peak arm velocity with time for rightward yaw stimulation (slope = $-0.28^\circ/\text{s}$ per second; $P < 0.05$). This change in peak velocity corresponds to a percentage change of only about 5% from the 1st to the 4th reaching trial, where most of the change in curvature occurs, and so the change of forward arm velocity likely had only a minor effect on the reach curvature. We also tested for a correlation between the time of peak forward arm velocity and the time of maximum perpendicular (lateral) arm deviation. When curvature was highest (the first four trials), there was a weak correlation between the time of peak forward arm velocity and the time of maximum sideways arm deviation. Two subjects showed significant correlations (Spearman's $\rho > 0.46$, $P_s < 0.01$) while in the third the correlation was marginally significant ($\rho = 0.4$, $P < 0.06$).

Vestibular induced errors in the reach end-points are shown in Fig. 6: subjects tended to make shorter reaching movements with vestibular stimulation (Fig. 6a), particularly on initial trials, but reaches became longer as the vestibular stimulation decayed. If subjects expected a centrifugal force as a result of the vestibular stimulation, they might be expected to reach short of the target, and as the vestibular signal decayed, reaches would become longer. This change in reach length was confirmed by multiple linear regression analysis, which found that reach length increased at a rate of 0.10 cm/s ($P < 0.01$) for leftward stimulation and 0.069 cm/s ($P < 0.05$) for rightward stimulation trials. The overall difference between leftward and rightward conditions was significant, ($t = 2.6$, $P < 0.05$), but the interaction of stimulation direction and time on the distance error was not ($t = 1.1$, $P < 0.3$), indicating the difference between the two curves remained constant. The best-fit exponential curves produced time constants of 7.6 and 3.6 s (mean 5.6 s) for leftward and rightward vestibular stimulations, respectively.

Subjects reached to the right with rightward vestibular stimulation, and to the left with leftward stimulation (Fig. 6b). However, there is little overall trend for the lateral errors to change as the vestibular stimulation decreased. Excluding the first trials, the lateral errors appear to decrease with time for the leftward stimulation condition, although a similar trend does not occur for rightward stimulation trials.

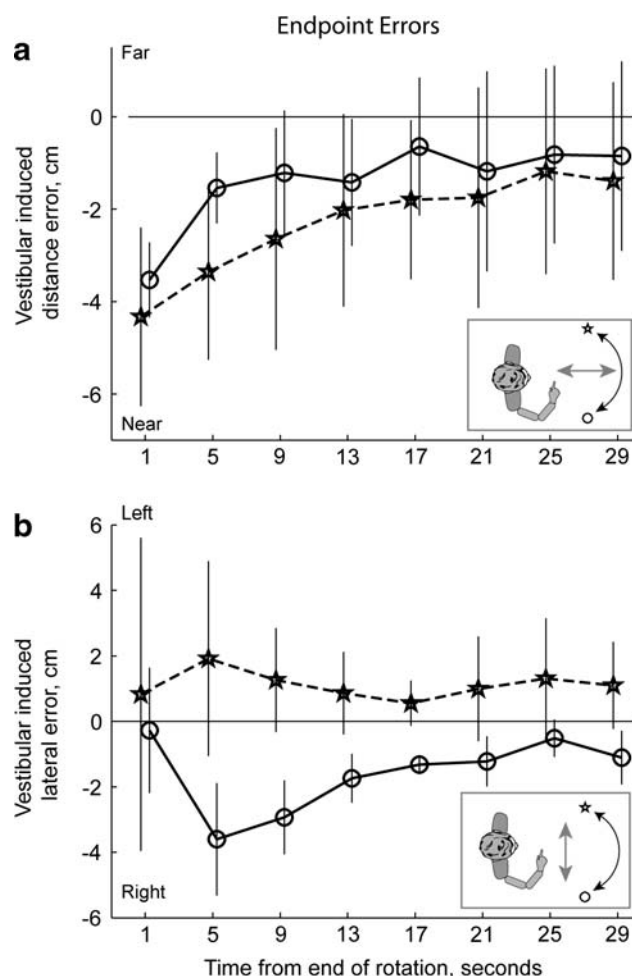


Fig. 6 Vestibular induced reaching errors. Stars denote data for leftward yaw stimulation, and circles indicate data for rightward yaw stimulation. **a** The average change in distance errors (vestibular trials compared to control trials). **b** The average change in perpendicular (lateral) errors. Points are averages, and error bars are ± 1 standard deviation

Experiment 2: preferred and non-preferred hand reaching trajectories are similar

The second experiment compared the effect of vestibular stimulation on preferred and non-preferred hands. In control trials without vestibular stimulation, reaching paths were generally straight, with average curvatures of -1.4 and 1.8 cm for preferred and non-preferred arms, respectively. The average peak forward velocity for control trials was 112.5 and 112.8 cm/s for preferred and non-preferred arms, respectively. For stimulation trials, the mean peak forward velocity was 114 and 110 cm/s for preferred and non-preferred arms, respectively.

Vestibular stimulation affected reach trajectories for preferred and non-preferred arms similarly. Figure 7a shows the curvature results for one subject, and Fig. 7b

shows the average of three subjects. The VIC for initial reaching movements was 3.17 cm for the preferred arm, and -3.27 cm for the non-preferred arm. In each case, the early curvature is in the direction of the vestibular stimulation, just as in the first experiment. A one factor ANOVA on the magnitude of the curvature (reversing the sign for the non-preferred arm) on the first trial found that the quantity of curvature for preferred and non-preferred arms was not significantly different ($F(1,30) = 0.02$, $P > 0.8$).

Exponential curves fit to the VIC found time constants of 3.7 and 1.8 s for preferred and non-preferred arms, respectively. Curvature in the non-preferred arm did not fully return to control values, as indicated by the -0.7 cm curvature offset. This likely contributed to the shorter time constant. Because subjects reached only every 4 s, our ability to precisely measure such fast time constants was limited.

Peak forward arm velocity tended to decrease with time for both the dominant (slope = $-0.51^\circ/\text{s}$ per second, $P < 0.05$) and the non-dominant arm (slope = -0.3723 ; $P < 0.01$). Further tests found that the difference between these slopes was almost statistically significant ($P < 0.06$). Over the first four trials, the peak arm velocity decreased by only about 4 and 5% for the non-dominant and dominant arms, respectively. Thus, the change in arm velocity likely had only a minor effect on the reach curvatures. One subject showed a correlation between the time of peak forward arm velocity and the time of maximum perpendicular (lateral) arm deviation ($\rho = 0.48$, $P < 0.01$), whereas the correlations were not significant for the other subjects (all P s > 0.4).

Figure 7c shows that the average reach was short of the target for both dominant and non-dominant arms, but reach length increased with time from the end of rotation. Reach lengths for dominant and non-dominant arms were significantly different ($t = 3.5$, $P < 0.01$), with the preferred arm being less affected. Multiple linear regression confirmed the significance for the increase in reach length for both dominant (slope = 0.076 cm/s, $P < 0.01$) and non-dominant (slope = 0.07 , $P < 0.01$) arms, and these slopes were not significantly different from each other ($t = 0.1$; $P > 0.9$).

Lateral errors were again fairly constant (Fig. 7d). For the dominant arm, there was a significant, although quite small decrease in lateral errors (slope = -0.052 cm/s, $P < 0.01$), while the trend for the non-dominant arm was not quite significant (0.039 cm/s, $P < 0.06$).

Discussion

We investigated whether the nervous system uses vestibular signals of head rotation to predict inertial forces that

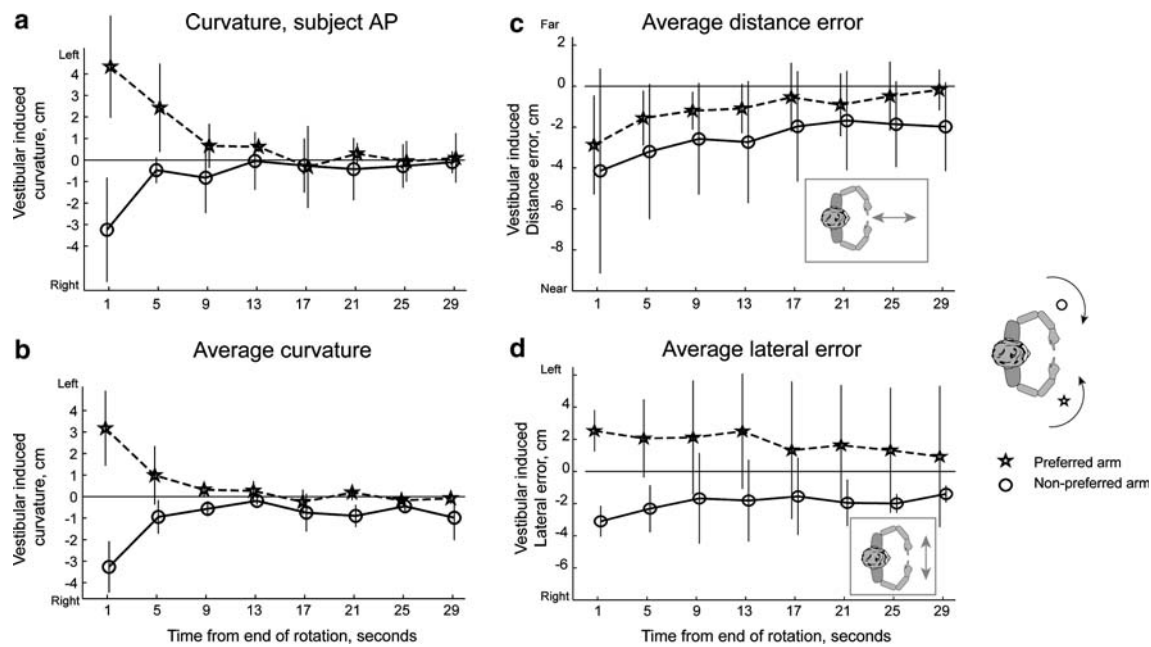


Fig. 7 **a** Vestibular induced curvature for subject AP when reaching with preferred and non-preferred arms. Each point is the mean of six reaches, and the error bars are ± 1 standard deviation. Points have been offset slightly from the actual trial number for clarity. **b** Average VIC

across all subjects. Each point is the average of three subjects, and the error bars are standard deviations. **c** Vestibular induced distance error. **d** Vestibular induced perpendicular (lateral) error

could influence reaching movements. We tried to design our paradigm such that the different factors contributing to the arm movement can best be separated. For inducing a strong movement sensation, we chose a stimulus that excites the vestibular system, our prime indicator of movement and orientation. We stimulated the vestibular system in a natural fashion and took advantage of the dynamic characteristics of the semicircular canals to show how canal-derived rotation signals influence reach planning. Specifically, in our paradigm the canals signalled a rotation when the body was in fact stationary, so the influence of vestibular cues could be investigated in the absence of the additional forces that are normally associated with body motion. Observed changes in reach movements could thus be directly attributed to the planned compensation for expected forces signalled by vestibular cues. Finally, to avoid visual feedback on the accuracy of the arm movement, we performed the reaching tasks in complete darkness.

Compensation for expected inertial forces

Our results show that in the presence of a vestibular yaw rotation signal from the semi-circular canals, the reaching movements are shortened and curved in the direction of the sensory rotation cue. Changes in reaching were largest when the vestibular velocity stimulus was greatest. The alterations in reach trajectories are consistent with the hypothesis that the subjects attempted to counter inertial

forces resulting from the perceived rotation. The curvatures suggest that subjects reach to counter an expected Coriolis force, while the shortened movements suggest subjects were anticipating a centrifugal force.

The analysis of the reaching trajectories also suggests that on-line corrections have a significant influence on the reaching path. Historically, feedback control for fast movements was not considered significant, although this view is changing (Desmurget and Grafton 2000; Flanders et al. 2003). Support for the hypothesis that on-line corrections play a larger role comes from several trajectory features. First, there is a low correlation between the time of peak forward velocity and the time of peak lateral displacement. If the lateral movement was dominated by the expected Coriolis force alone, a higher correlation between the two would be expected, as the Coriolis force is proportional to the peak forward velocity. Second, we sometimes observed secondary corrective movements at the end of the pointing trajectory, also suggesting some role for on-line correction. And third, the maximum curvature was similar in both paradigms, even though the vestibular stimulation was considerably different ($360^\circ/\text{s}$ vs. $200^\circ/\text{s}$): we hypothesize that an on-line error correction detects and compensates for trajectory errors early, resulting in smaller curvatures even for large vestibular stimuli. Lackner and DiZio (Lackner and DiZio 1994; DiZio and Lackner 1995) demonstrated that after subjects adapt to unexpected Coriolis forces, reaching movements made in the absence

of such forces are curved in the opposite direction as those performed during initial exposure to Coriolis forces. These curve trajectories rapidly become straight, leading Lackner and DiZio to speculate that limb position information from muscle spindles may be used to detect the deviant movement trajectories, leading to adaptation changes on subsequent reaches. We further suggest that the detection of aberrant limb position is used to correct on-going movements.

Reaching curvature in the first experiment returned to normal with a time constant of about 6 s. While this is shorter than the time constant of the yaw VOR, typically measured to be 12–20 s (Raphan et al. 1979), it is similar to the ~6 s time constant of the semi-circular canals. In the second experiment, where the vestibular stimulation was smaller than in the first experiment, the time constants were even shorter, 3.7 and 1.8 s for preferred and non-preferred arms, respectively. The short time constants suggest that manual control may be influenced directly by the canal signals, unadulterated by the velocity storage mechanism. The difference in time course could also be affected by proprioceptive information indicating that the arm is moving in an unintended direction. This feedback could be used to produce changes in subsequent reaching movements, as well as to trigger rapid on-line corrections. Arm velocity also tended to decline with time, which, even though the amount was quite small, would have tended to lead to smaller predictions of Coriolis forces, and perhaps decreased curvature too. Reaching movements became longer as the vestibular stimulus decayed, which is consistent with the nervous system predicting a centrifugal force caused by the rotation. The nervous system would program a reach to counter the expected outwardly directed centrifugal force, resulting in shorter movements. The multiple corrective movements we occasionally observed likely contributed to the variability in end positions, particularly the lateral positions. They may have been elicited by the mismatch between the expected and the sensed Coriolis force, which could have induced a re-interpretation of the torques produced at the joints by gravity and the movement of the different arm segments. The strong vestibular stimulus that we used can also be quite disorienting, and it seems likely that this produced inconsistent changes in localization, although mis-localization alone could not account for the curved trajectories. If people reach to a target that is stationary in the world while they turn, they should in fact reach to a different body-centred location. This is in fact the basis of a clinical test of vestibular dysfunction (Barany 1910), and has also been demonstrated with caloric (Karnath et al. 1994) and galvanic stimulation (Bresciani et al. 2002a; Mars et al. 2003), as well as reaching after passive rotation (Bresciani et al. 2002b).

While in our experiments the effect of expected but non-existent inertial forces was investigated, Lackner and DiZio studied reaching with real but un-expected forces (Lackner and DiZio 1994; DiZio and Lackner 1995). Using a slower rotation velocity of 60°/s, they found peak curvatures of 1.5 cm (1994 study; their ‘slow reach’ condition which had peak arm velocities similar to ours) and 2.1 cm (1995 study). We used a higher rotation velocity, and found slightly larger curvatures of 3.0 cm (Exp 1, 360°/s) and 3.2 cm (Exp 2, 200°/s). The time course of reaching changes is not directly comparable, because in our study the changes were due primarily to the declining rotation signal, whereas in the Lackner and DiZio studies the changes in reaching was due to adaptation to the real inertial forces. Lackner and DiZio also reported that initial reach movements tended to undershoot the target, whereas the presence of a real centrifugal force would cause movements to overshoot the target (Lackner and DiZio 1994; DiZio and Lackner 1995). Again, this could be caused by rapid on-line error corrective mechanisms shortening the reach movements. Our use of a higher rotation velocity, and so higher expected centrifugal force, may explain why we observe results consistent with a compensation for centrifugal forces. Their initial lateral errors were 4.1 and 2.7 cm, but in contrast to our general results, the lateral errors decreased with time, as a consequence of adaptation to the Coriolis forces. Why the lateral errors in our experiment generally did not change as the vestibular rotation cue reduced is unclear. Lackner and DiZio (1994) report that when subjects reached but did not make terminal contact with the touch board, endpoint errors did not adapt. Perhaps the latex finger worn by our subjects’ altered normal tactile cues when they touched, and this changed the normal calibration of felt arm position.

Our results complement those of Cohn et al. (2000) who showed that visual motion is used to predict Coriolis forces. We expect that the nervous system would exploit all sources of available information to improve motor performance, although vestibular signals would be particularly helpful in predicting inertial forces when people are passively rotated inside moving vehicles, because visual signals of movement can conflict with the actual movement. In the Cohn et al. (2000) experiments, both curvature and lateral errors increased with increasing visual rotation speed. In their fastest condition, simulating 120°/s of rotation, they found average curvatures of 2.6 cm and average lateral errors of 2.9 cm. With our faster rotation stimuli, we found maximum curvatures that were slightly larger and lateral errors that were of similar size. Reach length accuracy was not reported in their study.

Preferred and non-preferred arms use vestibular information in a similar fashion

We tested if vestibular signals differentially affect reaching with the dominant and non-dominant hand. Sainburg (2002) proposed that the dominant hemisphere may be specialized for controlling movement dynamics, whereas the non-dominant hemisphere is specialized for positional control. Evidence for this hypothesis comes from studies of multi-joint movements where performance depends on the compensation for interaction torques (Bagesteiro and Sainburg 2002; Sainburg and Kalakanis 2000) or external loads (Bagesteiro and Sainburg 2003). These studies indicate a superiority of the dominant hemisphere in the control of such movements. We therefore reasoned that the dominant hemisphere/hand might make greater use of vestibular information to predict Coriolis forces, and so we predicted greater curvature and distance errors when reaches were made with the preferred arm. We were wrong, as the vestibular stimulation affected preferred and non-preferred reaching in a similar way. It could be that the preferred arm has better access to proprioceptive information about reaching errors during a movement, and so could make more rapid and complete corrective reactions. This would also explain the smaller vestibular induced reaching errors by the preferred arm (Fig. 7c).

Neurophysiologic significance

Sensorimotor planning has been described as a cascade of coordinate transformations from target identification to specific muscle activation (Kalaska et al. 1997), and vestibular signals can affect this process at different stages (Bresciani et al. 2002b; Bresciani et al. 2005). First, vestibular signals of rotation can change an estimate of target location. Second, vestibular signals can affect the sensorimotor process that is used to control the reaching trajectory during rotations. We believe that the use of vestibular information to predict inertial forces would be most useful after target selection, when the expected Coriolis and centrifugal forces have to be considered in the correct execution of the intended arm movement.

For reaching movements, the target transformations have been associated with cortical processing streams passing from representations of intended targets in parietal cortex, through dorsal premotor cortex and then to primary motor cortex (Johnson et al. 1996; Wise et al. 1997). While there is no strict hierarchy, neurophysiologic evidence suggests that neural activity in primary motor cortex is more closely related to the execution of movements than to the selection of targets, whereas premotor and parietal regions show the reverse behaviour (Hatsopoulos et al. 2004; Kalaska et al. 1990; Scott et al. 1997; Scott and Kalaska

1997). Coriolis forces only occur during movements and depend on dynamics that derive from target location, and centrifugal forces also depend on target location. If we assume that the planned movement trajectories are unchanged during rotations, then compensation for inertial forces might occur relatively late, perhaps during the planning of movement dynamics. Consistent with the proposal of Bresciani et al. (2005), we expect that vestibular signals influence many stages of reach planning and execution. Vestibular signals have indeed been found in parietal cortex (Kawano et al. 1984; Bottini et al. 1994; Hietanen and Perrett 1996; Andersen et al. 1999). More importantly for the present results, tracer (Guldin and Gruesser 1998; Guldin et al. 1992) and multi-unit recording studies (Huffman and Krubitzer 2001) indicate a convergence of vestibular and hand somatosensory signals in area 3a. Area 3a also has strong connections with primary motor cortex and the supplementary motor area (Huffman and Krubitzer 2001), and in humans, fMRI studies have found that galvanic stimulation excites an area probably analogous to 3aV in monkey (Lobel et al. 1998).

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